Grazing and Orthoptera: a review

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Academic editor: *Corinna S. Bazelet* | Received 2 May 2018 | Accepted 2 June 2018 | Published 12 June 2018

http://zoobank.org/FCC5EA33-78A6-42B9-BEDF-0C99ED3A6C3F

Citation: Gardiner T (2018) Grazing and Orthoptera: a review. Journal of Orthoptera Research 27(1): 3–11. https://doi.org/10.3897/jor.27.26327

Abstract

Orthoptera are an important biological component of grasslands as a crucial link in the food chain. Grazing, either by wild animals or livestock for human food production, exerts considerable influence on the Orthoptera of grasslands. For example, grazing prevents succession of open grasslands to scrub and forest, creates heterogeneity in sward height, and provides patches of bare earth through the action of livestock hooves breaking the vegetative cover. Grazing may also interact with other forms of grassland management such as burning to produce quite complex interactions which vary greatly between regions and Orthoptera species. Threats to grassland Orthoptera include overgrazing; conversely, abandonment of grazing can lead to the loss of open habitats vital to many species. It is important to have ungrazed areas to provide refuges for species negatively affected by grazing. Rotational management – moving domestic livestock between different pastures – will also allow a range of sward structures to develop over a landscape. The over-arching principle for grazing management should be to establish a heterogeneous sward with a range of sward heights and bare earth for oviposition/basking. In more extensive systems, patches of scrub can form habitat of woody vegetation for species such as bush crickets. The greatest diversity of habitats should provide the highest species richness.

Key words

conservation, ecosystem, grassland, habitat, management

Introduction

Grasslands are one of the most extensive and important ecosystems. Grasses originated in the late Cretaceous period and, by the Miocene, grasslands were a prominent component of the earth's vegetation (de Wet 1981). It is estimated that grasslands now cover approximately 40% of the earth's land surface (White et al. 2000) and co-evolved with the grazing animals which maintain them in an early successional stage (Singh et al. 1983). Grasslands are a source of grass crop plants (grains) and herbivore products (fibre and meat), essential for the earth's expanding human population (Foley et al. 2011). Many grassland ecosystems have been altered by human activities and as such are considered 'semi-natural.' Grasslands are threatened by conversion to arable cropping (Suttie et al. 2005) and the pressures on those remaining from intensive agricultural practices such as overgrazing or, conversely, from a lack of grazing management leading to woodland encroachment, are great.

Grasslands are found in temperate and tropical regions on all continents except Antarctica, and can be classified into many different types including chalk downland, tallgrass prairie, savanna and shrubland steppe. In this review, grasslands are defined as "land on which the vegetation is dominated by grasses" (FGTC 1991) and no distinction is made between the types. Orthoptera form an important part of grassland ecosystems across the earth, consuming between 0.3–8% of net primary production (Köhler et al. 1987), although they are particularly wasteful feeders (e.g. *Chorthippus parallelus* consumes 2% of net primary production, but wastes 8%; Ingrisch and Köhler 1998). Orthoptera are also particularly important in food chains (Latchininsky et al. 2011), as prey for spiders and avian predators, for example. From an assessment of the status of European Orthoptera, 555 species (51.3%) were found in grassland, underlying the importance of the habitat (Hochkirch et al. 2016).

While Orthoptera can be used as indicators of healthy grassland ecosystems (Kati et al. 2004, Gardiner et al. 2005, Bazelet and Samways 2011), locusts are also an abundant pest in the rangelands of the USA and the arid grasslands of Africa, for example. Significant time and expense is invested in the control of locust outbreaks (Latchininsky et al. 2011) which can have negative effects on other fauna in the grassland ecosystem.

Grazing (by both domesticated and wild animals) effects properties of grasslands which are crucial for grasshopper life history processes. Intensity of grazing, type of grazer, rotational or seasonal aspects of the grazing regime, and the interaction of grazing with other grassland management practices, has an impact on characteristics of grasslands such as vegetation height, biomass, and plant species. In turn, these factors can influence oviposition, dispersal and feeding behaviors of grasshoppers, thereby affecting the dynamics within Orthoptera assemblages and communities. The aim of this paper is to provide a short introduction to grazing and its effects on Orthoptera, setting the scene for the more focused papers that follow.

Ecology of Orthoptera in grazed grasslands

Habitat preferences of Orthoptera may relate to choice of oviposition site, food preferences, vegetation height and biomass, and grassland management regimes (Clarke 1948). Waloff (1950) stated that the egg-pods of *Chorthippus albomarginatus* are oviposited into the base of grass lamina, while *Chorthippus brunneus* and *Chorthippus parallelus* lay their egg-pods in the superficial layers of the soil. Bare earth (often exposed in ant hills) is the usual egg-laying site for *C. parallelus*, although this species and *Omocestus viridulus* have been found to oviposit into grass-covered soil (Waloff 1950). All these oviposition niches are influenced by grazing, either for agricultural production or of wild animals.

An important distinction was made by Waloff (1950) in characterizing grasshopper species as either hygrophilous (egg-pods in vegetation just above soil: e.g. *O. viridulus*) or mesophilous (egg-pods laid in soil: e.g. *C. brunneus*). Grassland management such as heavy grazing may remove or damage egg-pods of hygrophilous species laid in the vegetation while leaving those of mesophilous species in the soil undamaged.

Choudhuri (1958) investigated the oviposition habits of *C. brunneus* and *C. parallelus*, concluding that *C. parallelus* preferred to oviposit in moist sand, while *C. brunneus* mostly laid eggs into dry sand. Compaction, temperature, moisture content and particle size of the soil were also found to influence the choice of oviposition site (Choudhuri 1958). Exposed soil may offer other benefits for grasshoppers by providing sites where they can bask (Key 2000), as exposed soil is often much warmer than surrounding vegetation. Trampling of the soil surface by grazing animals can create suitable oviposition sites for a range of species, and the type of livestock is important. For example, on sea walls cattle can produce a sward with a higher amount of bare earth than sheep due to their heavier nature (Gardiner et al. 2015), providing suitable niches for oviposition (Fig. 1).

The food preferences of *C. brunneus* and *C. parallelus* have been examined in some depth by Clarke (1948), Richards and Waloff (1954) and Bernays and Chapman (1970a, b). Clarke (1948) and Richards and Waloff (1954) suggest that the availability of suitable food (in respect of nutrient availability and palatability) may not be a limiting factor for British grasshoppers. However, Bernays and Chapman (1970a) found that *C. parallelus* selected grasses in preference to herbs for feeding. This selection could be due to a natural chemical on the leaf surface of grasses which induces biting. Bernays and Chapman (1970b) noted that fine-leaved grasses of the genera *Agrostis* and *Festuca* were often selected in preference to *Holcus*, *Cynosurus* and *Dactylis* by *C. parallelus* (Bernays and Chapman 1970b). Gardiner and Hill (2004), however, found a preference for coarse grasses such as *Dactylis glomerata* and *Lolium perenne* over the fine-leaved *Festuca rubra* and *Cynosurus cristatus*. Both *D. glomerata* and *L. perenne* are grass species that are commonly sown for agricultural purposes in pastures due to their high nutritive value to grazing livestock (Spedding and Diekmahns 1972, Hubbard 1984), although the former species is currently sown less than in the early 1900s (Hubbard 1984). It is suggested that these grasses were also preferred by *C. parallelus* because of their superior nutritive value and palatability.

Vegetation structure is an important factor for grassland fauna (Duffey et al. 1974, Morris 2000), particularly for grasshoppers. Clarke (1948) and Gardiner and Hassall (2009) noted that vegetation height and density are the most important habitat factors for grasshoppers, particularly in respect to their influence on microclimate.

Fig. 1. Cattle trampled ground with an abundance of bare earth, credit T. Gardiner.

Vegetation which is dense and tall is not readily warmed by the sun or cooled by free circulation of air, in contrast to sparser vegetation which provides better conditions for diurnal activity (Clarke 1948, Gardiner and Hassall 2009). Dense vegetation with high percentage cover, however, provides abundant food sources. Therefore, grasshoppers may be abundant in habitats which possess both dense vegetation and areas of sparser vegetation, and such local differentiation of vegetation structure may be important (Clarke 1948, Gardiner et al. 2002). Heterogeneity of sward structure may be important for other invertebrates such as butterflies (Ausden and Treweek 1995) and can be produced through rotational mowing, which creates a mosaic of cut and uncut areas (English Nature 1992), or extensive grazing regimes (Crofts 1999). Grazing that creates the small-scale patchwork of bare ground, low, herb-rich turf, and taller, tussocky grassland occurring in close proximity, is necessary for the conservation of the bush cricket *Decticus verrucivorus*, which can be easily lost due to even slight changes in management.

Gardiner et al. (2002) in a survey of grasslands in the Chelmsford area of Essex in the UK identified the optimum sward height and vegetation composition for three *Chorthippus* species. Grasshoppers were most abundant between vegetation heights of 100–200 mm (Gardiner et al. 2002), and in grasslands dominated by fine-leaved grass species such as *Agrostis stolonifera*. The findings detailed in Gardiner et al. (2002) agree with the conceptual model outlined in van Wingerden et al. (1991a) which visually displayed the relationship between grasshopper abundance and quantity of vegetation as an optimum curve.

Vegetation structure may influence egg development (van Wingerden et al. 1991a). Tall vegetation could lead to lower maximum temperatures in the soil surface and consequently delay hatching of eggs laid in the soil, resulting in a loss of some mesophilous grasshopper species (van Wingerden et al. 1991b). Such tall grasslands may be described as 'cold', while those with shorter, sparse vegetation are 'warm' (van Wingerden et al. 1991b).

Clarke (1948) suggested that vegetation height and density may be related to the following three factors: growth form of component plant species, properties of the soil, and grazing and other biotic factors such as trampling.

Factors influencing the abundance and behavior of Orthoptera in a grassland sward are complex and inter-related. To reflect this

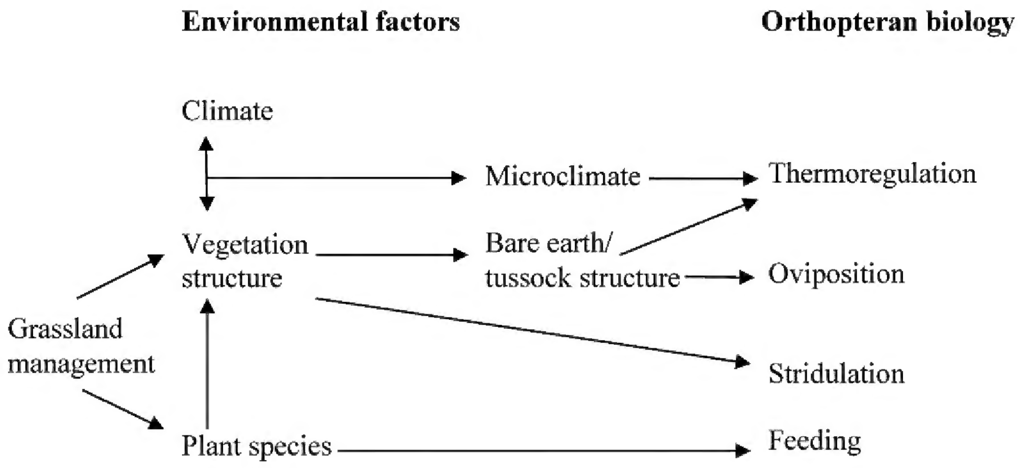

Fig. 2. Relationships between environmental parameters and the main behavioral activities of Orthoptera in a grassland sward (after Gardiner 2009).

complexity, Fig. 2 shows how the behavioral activities of Orthoptera may be affected by environmental parameters in a grassland sward (Gardiner 2009). Many of the environmental parameters presented in Fig. 2 are altered by grassland management such as grazing; therefore, in the field, Orthoptera will be affected by the interaction between management and environmental factors. For example, grazing will remove large quantities of herbage biomass and reduce sward height in the short-term, which may create a warmer microclimate which is more conducive to basking. Additionally, grazing may create patches of bare earth (through trampling of the soil by hooves) that provides a better environment for oviposition and basking purposes. I suggest that sward height and biomass are pivotal in determining suitability of grassland for Orthoptera due to their influence on many other environmental parameters such as microclimate, behavioral activities of individuals, and the abundance of grasshoppers (Gardiner 2009). Grassland management such as grazing is concerned mainly with the removal of the harvestable standing crop (Hopkins 1999) and is therefore crucial in determining the habitat preferences of Orthoptera.

Behavior and dispersal in grazed environments

Narisu et al. (1999) suggested that directional movements of grasshoppers in rangeland habitats may be related to the direction of the prevailing wind. In their study, adults moved predominantly into the prevailing north-westerly wind and it was suggested that the movement upwind may have reflected the search for resources such as feeding sites or mates. In the study reported by Gardiner and Hill (2004), both nymphs and adults of *C. parallelus* displayed directional dispersal within a small area of extensively-grazed pasture and a high proportion of adults and nymphs were re-observed in pasture north-west of the release site which was neither into or with the prevailing wind. The release area had been heavily grazed by sheep and the sward height in this area was below 50 mm (Gardiner and Hill 2004). Gardiner et al. (2002) suggested that *C. parallelus* is less abundant in short (<100 mm) vegetation. Therefore, the release circle was unsuitable for this species, having a short sward that provides no cover from avian predators or inclement weather conditions. This heavily grazed environment was 'spatially hostile' (Rogers 1984) for both *C. parallelus* nymphs and adults. Both life stages would therefore have a greater chance of survival and breeding success in a more suitable environment, and dispersal away from the release circle was a necessity for large proportions of the marked population in this heavily grazed pasture.

Horn (1984) suggested that the dispersal of grasshoppers is favored when the local environment is deteriorating, especially if more suitable conditions exist in other adjacent areas. Furthermore, patches that form in areas contaminated by feces or in latrines are avoided by most grazing livestock and have taller vegetation (Duffey et al. 1974, Ausden and Treweek 1995). Grasshoppers may actively seek out these areas for shelter and breeding sites in particularly unfavorable pastures. However, these patches of tall grass are only a temporary habitat and may be removed at any time if grazing pressure increases, which may lead to frequent movements of grasshoppers between favorable areas of tall grass and potentially unfavorable areas in relation to the rate of defoliation by the grazing animal (Gardiner 2015).

For successful migration, grasshoppers must have had some indication of the favorable habitat in the direction of travel. The compound eyes of orthopteroids are quite efficient at detecting movement (Marshall and Haes 1988) and it is reasonable to suggest grasshoppers can detect the long grass by its movement in the wind. Grasshoppers can judge the distance of long grass and singing perches by undertaking peering movements while assessing the suitability of a patch of vegetation (Chapman 1998). Nymphs and adults may be able to quickly assess distance and direction of suitable ungrazed patches of grass using their extensive 360° vision (Chapman 1998), particularly as peering movements would be unobscured by tall vegetation structures in heavily grazed habitats. Further neurobiological and behavioral research is needed to determine whether Orthoptera can see patches of suitable habitat and orientate towards them.

Other factors may also play a role in the dispersal of Orthoptera in grazed habitats. For example, sheep grazing may disturb nymphs and adults, leading to greater dispersal in a particular direction, or they may act as a transportation mechanism (Fischer et al. 1996). Grazing animals such as cattle could also 'flush' grasshoppers into pools within grasslands or heathlands, initiating swimming or drowning (Gardiner 2009).

The effect of grazing

Grazing intensity.—Grazing and trampling exert important influences on vegetation structure (Clarke 1948). Heavy grazing by cattle and sheep on fertile soils can produce a short, dense sward of neutral grassland species such as *Lolium perenne*, which is unsuitable for grasshoppers (Gardiner et al. 2002). However, Clarke (1948) suggested that excessive grazing by rabbits on chalk grassland and heaths promoted sparser vegetation, comprised of less vigorous species such as *Festuca ovina*, which was consequently more favorable to grasshoppers.

In another study on a heavily rabbit-grazed calcareous grassland, *C. brunneus* was more abundant within an exclosure than on the surrounding grazed grassland (Grayson and Hassall 1985). The authors suggested that the taller vegetation in the exclosure provided better cover from vertebrate predators and better quality food resources for grasshopper nymphs than the shorter grazed vegetation. In coastal pastures which have been ungrazed for many decades on Skipper's Island in southern England, the species richness of orthopteroids is higher than in mainland habitats such as sea wall flood defenses where mowing management is undertaken (Gardiner and Ringwood 2010). These ungrazed pastures have developed a mosaic of tussocky, rank grassland and scrub which is suitable for grasshoppers and bush crickets.

A large mesa in South Africa acted as a refuge for Orthoptera in comparison to the heavily grazed flatlands which surrounded it (Gebeyehu and Samways 2006). The summit, which was inaccessible to grazing livestock, was an important conservation refuge for one grasshopper species, *Orthochtha dasycnemis*.

Across Europe, overgrazing (particularly by cattle) is the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016). In the UK, concerns have been raised about the negative effect of pony overgrazing upon the orthopteran assemblages of the New Forest (Tubbs 1986, Pinchen 2000, Denton 2006). Denton (2006) outlines the importance of exclosures, from which grazing ponies are largely excluded, for Orthoptera in the forest. For example, both the nationally scarce *Omocestus rufipes* and *Nemobius sylvestris* are found in exclosures, the varied and taller vegetation structure created in the absence of excessive grazing being particularly important. Surveys along the Mardyke River Valley in the UK also showed that Orthoptera were extremely scarce in intensively grazed horse pastures and that species richness was lower than in ungrazed grassland (Gardiner and Haines 2008). The horses grazed continuously throughout the year on the south side of the Mardyke and this led to an extremely short sward (<100 mm in height) that may have provided insufficient cover from inclement weather and predators (particularly birds) for Orthoptera (Gardiner et al. 2002).

A study of rangeland grasshoppers in the USA found that most grasshopper species were more abundant on ungrazed treatments when compared to heavily grazed areas (O'Neill et al. 2003). However, one species, *Aulocara elliotti*, a serious pest of rangelands, preferred the heavily grazed plots, perhaps due to its exclusion from densely vegetated pasture. Conflicting evidence is provided in Holmes et al. (1979) who stated that some grasshopper species were more abundant in heavily grazed fields when compared with lightly grazed fields, while other species exhibited the opposite preference for infrequently grazed pastures with tall and dense vegetation. Cease et al. (2012) also demonstrated that abundance of the locust *Oedaleus asiaticus* was promoted by heavy grazing in north Asian steppe grasslands by the lowering of plant nitrogen (N).

In savannah grassland in South Africa, abundance and guild structure of grasshoppers varied between lightly and heavily grazed areas (Prendini et al. 1996). The heavily grazed areas characterized by short vegetation were dominated by grasshopper species associated with short grass and/or bare earth, whereas the lightly grazed grassland with taller and thicker grass had mainly grasshoppers of taller vegetation which were mixed feeders or tough grass feeders (Prendini et al. 1996).

Interaction with burning.—Fire and grazing are two of the main methods of grassland management, and in many areas they interact to influence populations or assemblages of Orthoptera. In Afromontane grasslands in South Africa, grasshopper abundance benefited greatly from burning and cattle grazing (Joubert et al. 2016). Most grasshoppers favored recently grazed or burned grassland, although some did not, further highlighting the species-specific response to grazing management observed in other studies.

In the UK, traditional Culm grassland management, such as grazing and burning, has been undertaken to restore neglected sites (Wolton 1991). Grazing of pastures usually occurs between late May and late September, at a stocking rate of approximately 1 suckler cow per ha over a period of 20 weeks, leading to a diverse sward about 150 mm in height (Wolton 1991). Winter burning (known as swaling) during January or February is also practiced and has traditionally been used after particularly wet summers when it is impossible to graze livestock. This burning reduces the quantity of leaf litter, therefore providing a more open sward (Ausden and Treweek 1995). The complex interaction between weather and grassland management has important effects on Orthoptera populations.

In a small-scale study of formerly grazed Culm grasslands subjected to burning, there was increased Orthoptera abundance (density 29X greater on burned plots than on unburned replicates) in the post-burn year (Gardiner et al. 2005), as in the studies of Samways (1994) and Bieringer (2002). It is likely that mesophilous species such as *C. parallelus*, which overwinter as egg pods in the soil, may escape the main destructive impact of winter burning. The reduced sward height/biomass and increased light penetration on winter-burned swards in April/May could lead to enhanced post-diapause development and basking opportunities for hatched nymphs. Recently-burned ground could also be attractive to melanic groundhoppers (*Tetrix undulata*; Gardiner 2012) and grasshoppers (*Myrmeleotettix maculatus*; Gardiner 2014). Grazing in the post-burn year could keep the vegetation open and prevent development of a tall, tussocky *Molinia caerulea* sward.

Hochkirch et al. (2016) suggest that wildfires are a significant threat to 173 European Orthoptera species, with bush crickets (Tettigoniidae) more threatened than grasshoppers (Acrididae), perhaps due to many bush cricket species being flightless and unable to escape from the flames.

Abandonment of grazing.—As most grassland exists at a relatively early stage of succession, abandonment of grazing can be particularly harmful to the Orthoptera assemblages reliant on the open sward, with 148 European species affected (Hochkirch et al. 2016). In Epping Forest in the UK, the locally-scarce grasshopper *O. viridulus* was significantly more abundant on cattle-grazed sites than in ungrazed grassland and heathland (Gardiner 2010). The absence of grazing in particular, led to scrub encroachment and natural woodland succession throughout the open plains in the forest, causing major declines in floristic and thermophilous insect diversity in the 20th century (Rackham 1986). Despite these losses, Epping Forest is still considered one of the most important areas for Orthoptera in Essex County (Wake 1997), with new species such as *Stenobothrus lineatus* colonizing the open plains (Wilde 2009), perhaps in response to climate change (Gardiner 2009).

Rare species in the UK, such as *D. verrucivorus*, which are on the edge of their range, have very specific micro-habitat requirements (Cherrill and Brown 1990, 1992). *D. verrucivorus* was formerly found on several heathland sites in southern England, but with the loss of these populations, it is now restricted to ancient calcareous grassland (Fig. 3). *D. verrucivorus* disappears very quickly if winter-cattle-grazing ceases and tall rank grasses such as *Brachypodium pinnatum* encroach onto the bare ground. These rank grasses replace the low, herb-rich turf that *D. verrucivorus* requires for oviposition and which its early nymphal stages require for quick development in the warm microclimate provided by the open niches of this turf (Sutton 2015).

Conversely, abandonment of cattle livestock grazing in Spanish grasslands had an immediate positive effect on density, diversity and species richness of Orthoptera, although the effects were species-specific (Isern-Vallverdu and Pedrocchi 1994). The ungrazed pastures had taller grasses which were generally more favorable for Orthoptera because they had more refuges than the formerly grazed habitats. Species which benefitted from abandonment of grazing in Isern-Vallerdu and Pedrocchi's (1994) study included *S. lineatus* and large species such as *Platycleis tessellata* which needed the cover from avian predation. One species which was associated with short grassland and bare ground, *M. maculatus*, disappeared with the abandonment of cattle grazing. This may explain its extirpation from Epping Forest in the UK where cattle grazing ceased

Fig. 3. Grazed chalk downland in Sussex, UK, habitat for the rare *Decticus verrucivorus*, credit T. Gardiner.

Fig. 4. Cattle grazed wet grassland in Epping Forest, UK, habitat for *Omocestus viridulus*, credit T. Gardiner.

in the 20th century, although cattle grazing was reintroduced in 2002 and has since been linked to an increase in abundance of *O. viridulus* (Gardiner 2010; Fig. 4).

Type of grazing animal.—The type of grazing animal has widely differing impacts on the sward structure of grassland. Large-scale cattle grazing in Georgia led to a mosaic of grassland, scrub, and trees, offering habitats for several highly specialized species of Orthoptera (Bontjer and Plachter 2002). However, contradictory evidence is provided by a study of vegetated sea wall flood defenses in the UK (Gardiner et al. 2015). On two cattle-grazed sea walls which had fairly short swards (<10 cm in height) with few grass tussocks, abundance of grasshoppers was lower than on the ungrazed sea walls which had higher densities and more variation in sward height (10–40 cm). This suggests that the impact of heavy cattle grazing, which leads to very uniformly short swards, is not favorable for *Chorthippus* grasshoppers which require tussocks of tall grass for shelter and feeding. However, on the sheep-grazed sea walls, which had greater variation in sward height (10–30 cm) than the cattle-grazed sections, abundance of grasshoppers was higher than in the ungrazed control swards which were quite uniformly tall and rank in nature (>40 cm in height). Therefore, the impact of grazing on grasshoppers is likely to be through the establishment of suitable sward heights at appropriate stocking rates, with light sheep grazing producing more variation in vegetation height than cattle grazing where swards can be uniformly short due to high stocking rates (Gardiner et al. 2015).

Fonderflick et al. (2014) found that that the impact of sheep grazing exerted a species-specific influence on the grasshopper assemblage, which varied greatly over the season in Mediterranean steppe-like grasslands. They concluded that extensive grazing by sheep tended to homogenize the vegetation structure and led to a temporary reduction in Orthoptera abundance at a pasture scale. Fonderflick et al. (2014) suggested that rotational grazing systems could conserve Orthoptera at a farm scale by promoting heterogeneity in sward structure. Irregular grazing, likely to produce a sward with greater sward heterogeneity, was also found to have significantly higher species richness of Orthoptera (28 species) than plots with mown grass (17 species) or permanent sheep pens (14 species) (Fabriciusová et al. 2011). Species-specific responses to grazing were also noted in submontane pastures in the Hrubý Jeseník Mountains in the Czech Republic, where the abundance of *Gomphocerippus rufus* increased substantially with grazing, which contrasted with *G. rufus*' negative response to mowing (Rada et al. 2014).

In subalpine pastures in the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois). However, they did observe the small-scale alteration of habitats and plant N content by ungulates, which in turn affected Orthoptera abundance and diversity.

Intensive grazing by unmanaged wild rabbit, *Oryctoloagus cuniculus*, populations in Epping Forest in the UK, led to the extirpation of *O. viridulus*, a grasshopper with a preference for tall grassland (Gardiner 2010). The grazing created a very homogenously short grassland sward resembling a 'lawn' which consequently did not provide the necessary shelter or 'cool' microclimate for *O. viridulus*.

In Europe generally, there has been a move away from traditional sheep and goat farming to cattle grazing, leading to fewer and larger farms, with overgrazing a significant issue (Hochkirch et al. 2016). While this process was well underway during the middle of the 20th century in north-west Europe, it has now spread to Mediterranean areas and the new Member States of the eastern European Union.

Agricultural improvement of pastures – Orthoptera in decline?—The effect of agricultural improvement of grasslands on Orthoptera has received little attention when compared to other aspects of farmland management in Europe in particular. One study detailed the effects of fertilization on the species composition and abundance of grasshoppers in the Netherlands (van Wingerden et al. 1992). In this study, overall grasshopper density and species richness decreased with increased fertilization, perhaps due to the higher herbage biomass and denser structure of the sward in the fertilized plots which created a 'cold' sward, unsuitable for diurnal activities such as basking of nymphs/adults or egg development.

The studies conducted by van Wingerden et al. (1991a, b, 1992) in the Netherlands, and research in the UK by Clarke (1948) and Gardiner et al. (2002), would seem to suggest that herbage height and biomass are important factors that regulate the abundance of grasshoppers in grasslands. Based on these studies, we would expect management which reduces herbage biomass to affect grasshopper abundance as outlined in the simple conceptual model in Fig. 5. The model attempts to portray the highly complex relation-

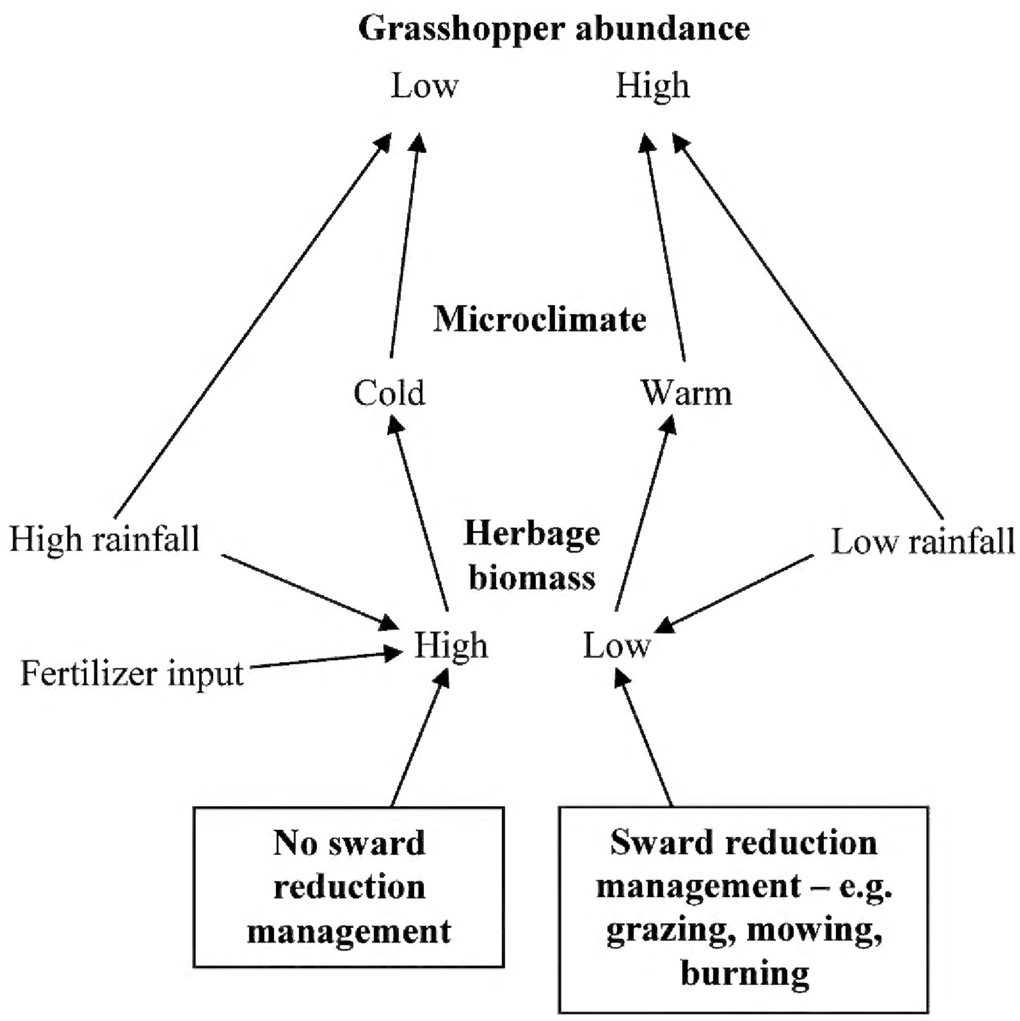

Fig. 5. A simplified conceptual model of the possible effects of management to remove herbage biomass and lack of management on grasshopper abundance (the effects of fertilizer input and rainfall are added to provide a more holistic approach) (after Gardiner 2009).

ship between management which reduces the standing crop, and grasshopper abundance, in a simplified manner.

This model illustrates that lack of sward reduction management leads to higher herbage biomass, which, in turn, leads to a 'cold' microclimate and lower grasshopper abundance. This trend can be exacerbated by fertilizer input and high rainfall, which would both contribute to an increase in herbage biomass. Alternatively, sward reduction management actions such as grazing, mowing, and burning, can be expected to lead to low herbage biomass, a warmer microclimate, and higher grasshopper abundance. This, in turn, can be exacerbated by low rainfall in a certain year (Fig. 5).

Any research into the temporal changes in Orthoptera communities in agricultural habitats should consider the economic constraints of agricultural management. The primary objective of grassland farming, which accounts for approximately 66% of land use in the UK, is to produce high livestock yield to serve the consumer food chain (McInerney 1995). This is often produced through optimizing grass yields with the application of nitrogen fertilizer which may be detrimental to grasshopper abundance (Fig. 5).

Pasture intensification – a case study from the UK.—A study of intensive and extensive pasture in the UK (Gardiner 2009) showed that unfertilized extensive pastures led to enhanced species richness, assemblage diversity and increased nymphal and adult abundance of Orthoptera, particularly of the grasshopper species *C. albomarginatus* and *C. parallelus*. These results supported those of Kruess and Tscharntke (2002) and van Wingerden et al. (1991a) who concluded that species richness and abundance of Orthoptera, respectively, were higher on extensively-grazed pastures compared with intensively-managed grassland. Contradictory evidence was provided by Batáry et al. (2007), who found only marginally significant differences in the abundance of Orthoptera between intensively and extensively grazed grasslands in the Hungarian Great Plain. Other studies on the impact of extensive grazing on grasshoppers in Europe concluded that grasshopper diversity and abundance were higher at grazed sites compared with mown grasslands (van Wingerden et al. 1991a, Wettstein and Schmid 1999).

The intensively managed pasture in Gardiner (2009) may have been unfavorable for Orthoptera due to silage cutting during June and intensive (high stocking rate) grazing. Inorganic fertilization led to tall vegetation height in May which can create a 'cold' microclimate (low temperatures in intensive pasture) that is unsuitable for nymphal development or post-diapause development in the egg stage.

Assemblage diversity of Orthoptera was higher in the extensive, unfertilized pastures perhaps due to the presence of tussocky patches of grass in rejected areas created where dung was deposited (Gibson 1997). Rejected areas were not necessarily present in the intensive pasture due to the removal of most vegetation above 70 mm during silage cutting and subsequent heavy grazing. In the extensive pastures, rejected areas supported small populations of bush crickets (*Conocephalus discolor* and *Metrioptera roeselii*) and grasshoppers (*C. albomarginatus* and *C. parallelus*). The short vegetation between tussocks provided ideal 'warm' conditions for basking and development of nymphs, while the tall vegetation offered shelter from inclement weather and avian predation as well as feeding resources. It is possible that grasshopper species such as *C. parallelus* actively seek out these nutrient rich niches in extensive patches (Gardiner and Hill 2004, Gardiner 2015), and may have to move between tussocks in a season due to disturbance by cattle or sheep and subsequent removal of tussocks through defoliation (Gibson 1997).

Examination of the stocking rate in the extensively managed pastures showed they were continuously grazed at approximately 2–4 cows per ha. The stocking rate suggested by Crofts (1999) as favorable for conservation objectives is 2 cows per ha for a similar grazing duration (24 weeks). Gardiner (2009) decided on a higher intensity stocking rate than is indicated by the literature to test whether a more economically viable grazing system with a higher number of livestock per unit area could provide biodiversity benefits. Although both extensive pastures provided better habitat for Orthoptera than intensively managed grassland, the suboptimal sward heights (<100 mm) led to low orthopteran densities, particularly of grasshopper species such as *C. albomarginatus* and *C. parallelus*. A lower stocking rate (2 cows per ha) would have led to a relaxation in the grazing pressure (Frame 1992) and taller sward height, particularly in July and August. These swards may have provided a greater chance of refuge for adult grasshoppers and bush crickets. However, a trade-off must be considered between economic viability of the grazing system and biodiversity benefits. Since the extensive pastures provided larger numbers of Orthoptera and higher assemblage diversity than the intensive sward, the moderate-intensity stocking rate and grazing pressure were justified on financial grounds. The stocking rate of 2–4 cows per ha is only slightly lower than that suggested by Frame (1992) as the proper management of improved swards for optimal agricultural production (5–8 cows per ha). Pastures are often assessed by using target sward heights and, for improved grassland managed by continuous grazing, the target sward height is 60–80 mm for cattle (Frame 1992). In all years the extensive pastures had a mean sward height that was predominantly 60–90 mm, suggesting that they were managed at stocking rates which produced swards of acceptable height for good agricultural management.

The absence of inorganic fertilizer input on these swards may impact upon yields but not necessarily economic viability. For example, under silage cutting, inorganic fertilizer input may substantially increase dry matter (DM) production in grass/swards (Frame 1992, Tallowin et al. 2002) but beef cattle output on low input systems (restricted N input) and fertilized pastures (moderate N input) has been found to be very similar, suggesting that low input systems may not affect the economic viability of grazing, particularly in clover-rich swards [such as the extensive pasture in Gardiner's (2009) study] with high rates of nitrogen fixation (Frame 1992). Other studies confirm that absence of fertilizer input may not necessarily affect animal liveweight gain and may be comparable to conventional farming systems with a high nitrogen input (296 kg N per ha; Lawes et al. 1995). However, lack of inorganic fertilizer usage in the study of Lawes et al. (1995) did significantly reduce the quantity of herbage conserved, suggesting that silage cutting may not be viable on extensive pastures. The absence of silage cutting and fertilizer input on pastures would seem to be a key requirement for maintaining populations of Orthoptera, and we suggest that where conservation of insects such as grasshoppers and bush crickets is desired, then pastures should be managed by continuous, low-input grazing at a moderate stocking density (2–4 cows per ha) which produces a sward of 60–80 mm in height. A study of extensive pastures by Marriott et al. (2002) concluded that unfertilized herbage at a height of 80 mm with a high quantity of dead leaf material may not pose problems for livestock diet due to preferential grazing of green leaves.

Of course, the stocking rates and choice of livestock are greatly influenced by subsidies provided by governments or the Common Agricultural Policy (CAP) in Europe, for example. Many farmers in the EU receive payments to farm more sustainably.

Conclusions

It is not the purpose of this paper to provide a comprehensive overview of the effects of grazing on Orthoptera; this will be provided by the other contributions to this special issue. However, from this brief review of the literature, the following are key issues to be considered when determining the impact of grazing management on Orthoptera:

1. Response of Orthoptera assemblages and species to grazing differs depending on the region and type of grassland.
2. The effect of grazing on Orthoptera is largely species-specific.
3. The type of grazing animal influences Orthoptera abundance and assemblage diversity. Cattle and sheep can be important domestic grazing animals, but both have their advantages and disadvantages for Orthoptera conservation and pest management. Wild animals may also have an important impact on Orthoptera (e.g. rabbits and ungulates).
4. Agricultural improvement (inorganic fertilizer input, heavy grazing and ploughing) of many lowland temperature pastures has led to a decrease in their suitability for Orthoptera due to unfavorable sward structure and height.
5. Grazing can interact with other forms of management such as mowing and burning, producing complex effects on assemblages of Orthoptera.
6. It is important to have ungrazed areas to provide refuges for Orthoptera species negatively affected by grazing. This can be accomplished through fencing off grassland or open woodland to form exclosures, where practical.
7. Rotational management – moving domestic livestock between different pastures – allows a range of sward structures to develop over a landscape.
8. Latrines can be refuges for Orthoptera in pastures, providing tall grassland avoided by grazing animals. These may be actively sought out by grasshoppers dispersing through pastures to find favorable feeding patches.
9. Abandonment of grazing, leading to the development of rank grassland and, ultimately, woodland, can have devastating effects on species of early successional stages, such as the rare *Decticus verrucivorus*.

The over-arching principle for grazing management should be to establish a heterogeneous sward with a range of sward heights and bare earth for oviposition/basking. In more extensive systems, patches of scrub can form habitat for Orthoptera species associated with woody vegetation, such as bush crickets. The greatest diversity of habitats should provide the highest species richness at a landscape scale.

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